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Functional and evolutionary correlations of steep leaf angles in the mexical shrubland

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Running title: Leaf angle evolution and function.

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Abstract In the evergreen shrubland vegetation of Mexico (mexical), most of the species are sclerophyllous woody plants with steep leaf angles. This architectural pattern has been interpreted as a strategy to cope with water shortages and high radiation. However, the current association between evergreenness and steep leaf angles across mexical plant species could be the result of an adaptive association achieved through correlated evolutionary change between both traits or, alternatively, may be the result of common evolutionary ancestry**.**

In this study we quantified leaf angle in 28 dominant species under a phylogenetic framework and evaluated the functional implications of the observed range of leaf angles in terms of leaf temperature, water potentials and transpiration by combining manipulative experiments restraining leaves horizontally with microclimatic and stomatal conductance measurements in selected species and energy balance calculations.

Horizontally restrained leaves exhibited reduced water potentials and stomatal conductances, and significantly increased temperatures and transpiration rates. Steeply inclined leaves operated near air temperatures and could sustain relatively high stomatal conductances during the dry season since they were associated with low transpiration rates. Phylogenetic analyses showed that steep leaf angles evolved in a correlated fashion in evergreen species. The functional consequences of leaf angle together with the phylogenetic analysis indicate the adaptive nature of this trait which allows the evergreen species to cope with arid conditions and therefore to persist within the mexical community.

Key words: Mexical, phylogeny, stress avoidance, Tehuacán-Cuicatlán Valley, water potentials.

Introduction

The mexical vegetation is a relict of the Madro-Tertiary Geoflora whose patchy distribution along the rain-shadowed principal mountain chains of Mexico, in non-Mediterranean climates seems to be the result of the expanding dry climate during the Miocene epoch (Valiente-Banuet et al. 1998). Two of the most important traits of plants inhabiting seasonally dry habitats are evergreen and sclerophyllous leaves. These two leaf features together predominate in Mediterranean-type climates, as well as in the mexical vegetation. The mexical community assemblage is mainly composed of evergreen (82%) and sclerophyllous (79%) plant species. Interestingly, 93% of all evergreen and sclerophyllous species present vertically-oriented leaf angles (Valiente-Banuet et al. 1998). In contrast, the few deciduous species apparently do not show this pattern (Valiente-Banuet et al. 1998), probably because they avoid drought stress by shedding the leaves during the dry season. The current association between evergreenness and steep leaf angles across mexical plant species could be the result of an adaptive association achieved through correlated evolutionary change between both traits or, alternatively, may be the result of common evolutionary ancestry (i.e. all the evergreen species have steep leaf angles because they share a common evergreen ancestor with vertical leaves).

From a functional viewpoint, the predominance of steeply inclined foliage in arid environments has been interpreted as a strategy to cope with water limitations and high radiation loads (Falster and Westoby 2003). Steep leaf angles with respect to the horizontal plane considerably reduce heat-loads particularly at midday, decreasing the risk of over-heating and photoinhibition (Valladares and Pugnaire 1999), Likewise, species with steep leaf angles may be able to maintain increased levels of photosynthesis during high radiation periods (Falster and Westoby 2003) increasing water use efficiency (King 1997). All these advantages can have adaptive significance in arid environments due to their positive effects on reproduction output (Shaver 1978; Werk and Ehleringer 1986; Ehleringer

and Comstock 1987,1989; Smith and Ullberg 1989; Pearcy et al. 2005). High irradiance coupled with low water availability and a highly exposed foliage can lead to very low leaf water potentials, which have been associated with increased embolism risk in many species (Jarbeau et al. 1995; Redtfeld and Davis 1996; Jacobsen et al. 2005). Thus, steep leaf angles and consequent reduced radiation absorption constitute a crucial adaptation for surviving in arid environments, which has not been fully analyzed (Ehleringer and Comstock 1989).

From an evolutionary point of view, it is necessary to explore the statistical dependence derived from the phylogenetic relatedness of the species to test the relationship between evergreeness and leaf angle (Harvey and Pagel 1991). A first aim of this study, therefore, was to compare the pattern of leaf angle inclination between the most representative evergreen and deciduous species of the mexical under a phylogenetic framework. A second aim was to determine if the steep leaf angle found in most species of the mexical bestows an advantage to sclerophyllous-evergreen plant species by allowing the maintenance of higher water potentials, and lower temperatures and transpiration rates. We hypothesize that steep leaf angle is an important trait that has evolved in evergreen species allowing them to cope with arid conditions and therefore to persist within the mexical community.

Material and methods

Study site

The study was conducted in the Tehuacán Valley, located in south-central Mexico between the states of Puebla and Oaxaca (17º39´-18º53´ N; 96º55´-97º44´ W). The mexical vegetation in the valley is located in an altitudinal belt ranging from 1950 to 2500 m a.s.l. The climate is semiarid, with an average annual precipitation of 611.5 mm. concentrated in summer and mean annual temperature of 17.7 ºC (Fig. 1). The area represents the central part of a Cenozoic continental basin formed from an arm of the Cretaceous sea, and features calcareous mountains as high as 2900 m a.s.l. (Valiente-Banuet

et al. 1998). Soils are shallow and derived from limestone rocks. The vegetation is an evergreen sclerophyllous shrubland consisting of 225 species of seed plants, of which, shrubs (47%), ephemerals (39.2%), chamaephytes (10.8%) and trees (7.41%) predominate. This vegetation maintains old woody tropical lineages such as *Acacia, Amelanchier, Arbutus, Bursera, Ceanothus, Cercocarpus , Comarostaphylis* (= *Arctostaphylos*), *Garrya, Karwinskia, Leucaena, Litsea, Quercus, Rhus,* and *Satureja* (Valiente-Banuet et al. 1998; Lloret et al. 1999; Verdú et al. 2002, 2003). The vegetation is characterized by a 40-50% woody cover of predominantly sclerophyllous and evergreen plants leading to only one canopy layer, with subshrubs and herbs restricted to gaps.

Leaf-angle and evergreenness

A total of 28 dominant species in the Tehuacán Mexical were selected for leaf angle measurements. For each species we randomly sampled 10 plants of similar size and obtained the measurements from the five most exposed mature leaves on terminal branches. All measurements were done using a commercially-used protractor with a plumb line degree indicator (Mineola, N.Y.). The protractor has a ruler which was held up to each leaf and the angle between the leaf and the horizontal was measured to the nearest 0.5º. Data were analysed using Watson´s circular statistic analysis (Batschelet 1981), comparing the mean leaf angle between evergreen and deciduous species, under the null hypothesis that the mean leaf angle does not differ between them.

The phylogenetic association of evergreeness with leaf angle was tested by means of a Generalized Estimating Equation (GEE) procedure that uses a GLM approach incorporating the phylogenetic relatedness among species as a correlation matrix in the model. The GEE analyses were run with the "compar.gee" function within the APE package for R (Paradis and Claude 2002).

The phylogenetic relatedness among the 28 study species was determined with the help of the program Phylomatic as implemented in Phylocom 3.34b (Webb et al. 2005). This program returns a

working phylogenetic tree after matching the genus and family names of our study species to those contained in the angiosperm megatree (R20050610.new). This megatree is based on the work of the Angiosperm Phylogeny Group and represents a constantly-changing, working hypothesis (Stevens 2001). Some polytomies in our working tree resulted from the lack of information in the megatree. The branch lengths of our working phylogenetic tree were adjusted with the Bladj algorithm in the Phylocom 3.34b program (Webb et al. 2005). This method takes the age estimates for major nodes in our tree from Wikström et al. (2001) and distributes undated nodes evenly between nodes of known ages (See Moles et al. 2005 for a similar procedure). These methods must be treated as rough approximations that are prone to error and it is therefore very important to account for different sources of uncertainty (Donoghue and Ackerly 1996). To do this, we repeated the evolutionary correlation (i.e. GEE) test between evergreeness and leaf angle in 100 trees in which uncertainty on the topology of the phylogeny, the branch lengths and character scoring were simultaneously accommodated. Uncertainty on the topology of the phylogeny was accounted for by randomly resolving the polytomies of our working phylogeny using Mesquite 1.06 program (Maddison and Maddison 2005). Uncertainty on branch lengths was accommodated by adding random noise to branch lengths of the tree (Díaz-Uriarte and Garland 1998). Noise was normally distributed, with variance proportional to current branch length. A variance multiplier of 0.1 was entered to add to branch lengths. Thus, if branch length is 10, the noise added will have a variance of 1.0 (0.1 x 10). Uncertainty on character scoring (leaf angle) was accommodated by adding random noise to the mean leaf angle of each species. The mean and standard deviation of leaf angle within each species were used to generate the normally distributed random noise (see Verdú 2006 for a similar procedure).

Effects of leaf angle on water potential, leaf temperature and transpiration

Ten individuals of each of the five most dominant evergreen sclerophyllous species, *Citharexylum oleinum* (Benth.) Moldenke (Verbenaceae), *Comarostaphylis polifolia* (Kunth) Zucc. ex Klotzsch (Ericaceae), *Garrya ovata* Benth. (Garryaceae), *Quercus sebifera Trel.* (Fagaceae), and *Dodonaea* viscosa (L.) Jacq. (Sapindaceae), were selected in order to measure the effect of leaf angle on water potentials.All these species have small, simple, broadleafed leaves. Leaf angles were experimentally manipulated to restrain leaves horizontally by inserting an inert epoxic material between the leaf petiole and the branch. A control branch of the same height and with a similar number of leaves as the experimental branch was labelled on the same individual. Water potentials were measured after three days on both the experimental and control branches by means of a Scholander pressure bomb (PMS, 0-100 Bars, model 1000) between 11:00 and 15:00 hours. The experiment was carried out in the middle of the dry season (March of 1997). Data were analysed by means of paired t-tests for each species. The null hypothesis assumed equal water potentials between control and treatment branches.

The two most dominant species in the Tehuacan Mexical, *Quercus sebifera* and *Rhus standleyi*, were selected to measure temperatures in horizontally restrained leaves, and control, almost vertical leaves. Daily fluctuations of leaf and air temperatures were measured with copper-constantan thermocouples during the dry season. Measurements were taken every 5 seconds and the averages of 5 minutes were stored in Campbell Sci 21x dataloggers.

Leaf stomatal conductance around midday of clear days was determined during the dry season in seven representative species (*Garrya ovata, Rhus virens, Comarostaphylis polifolia, Dodonaea viscosa, Citharexylum oleinum, Rhus standleyi, Quercus sebifera*) with a portable infrared gas analyzer (LiCor 6200, Licor, Nebraska, USA). Measures were usually taken in 4-6 leaves from 2-5 individuals of each species. Stomatal conductance was measured in leaves at their normal elevation angles, and at vertical and horizontal angles. Stomatal conductance for deciduous species could not be determined

and was estimated from comparative studies of evergreen and deciduous woody plants co-occurring in similar ecosystems (Mediavilla and Escudero 2003). Climatic, morphological and physiological data were used to estimate leaf temperature and transpiration under clear sky conditions (2300 mmol m^{-2} s^{-1}, 1000 W m^{-2}) as a function of leaf angle and conductance using general energy balance equations (Nobel 1991). Plots of leaf temperature and transpiration as functions of leaf angle and stomatal conductance were made for two environmental conditions: a) mild and windy, air temperature of 25 ºC, soil temperature of 35 ºC, wind speed of 2 m s^{-1}, 45% of relative humidity of the air, and b) hot and still, air temperature of 35 ºC, soil temperature of 45 ºC, wind speed of 0.1 m s^{-1}, 20% relative humidity. Leaf absortance was taken as 0.84 for PAR (photosynthetically active radiation) and 0.6 for the full sun spectrum. Characteristic dimension was taken as 3 cm, which is a representative mean value for the species of the community.

Results

Leaf-angle variation and evergreenness.

Evergreen species presented significantly steeper mean leaf angles with respect to the horizontal than deciduous species ($F = 5.59$; d. f. = 54; $p = 0.02$; Fig. 2). This association was not a mere effect of common ancestry; it remained significant after statistical control of phylogenetic relatedness among species. The fact that the deciduous species are scattered throughout the phylogenetic tree in a seemingly random fashion (Fig. 3) provides visual corroboration of these analytical results. Also, evergreenness was evolutionarily correlated with leaf angle in 99 out of the 100 fully-resolved trees derived from our working phylogeny depicted in Fig. 3. The 99 significant GEE estimates pointed towards the direction of evergreens having steeper leaf angles than deciduous plants (statistical estimates of the models ranged from 11 to 39 and the associate p-values from 0.02 to

0.00002). Because the 100 derived trees simultaneously accommodated topological, branch length and character scoring uncertainty, the association between leaf angle and evergreenness is very robust.

Effect of leaf angle on water potential, leaf temperature and transpiration

Branches with horizontally restrained leaves presented significantly lower water potentials than control branches in all of the five species studied (Fig 4). Mean water potential values at midday ranged from -5.3 to -8.8 MPa in horizontally restrained leaves, whereas in control branches these values ranged from -4.7 to -8.6 MPa.

The temperature of vertical leaves was within 1 or 2 °C of air temperature diurnally in both studied species (Fig. 5 a, b). The temperature of fully exposed horizontal leaves, was 3 to 6°C above air temperature during most of the day. Maximum temperature reached in horizontal leaves were 26.5°C and 30°C for *Q. sebifera* and *R. standleyi* respectively, whereas the maximum air temperature was 21.7°C and 25.3°C. There was a 5°C difference in the maximum temperature between vertical and horizontal leaves.

Simulations of leaf temperatures for a range of leaf angles and stomatal conductances further confirmed that the steep leaf angle of evergreen species allowed them to operate near air temperature under both mild and windy, and hot and still conditions, while lower leaf angles such as those of deciduous species or horizontally restrained branches led to very high leaf temperatures (Fig. 6). Since horizontally restrained leaves exhibited a very low stomatal conductance, they are prone to experience extremely high temperatures (> 45 ºC), while the reverse was true for vertical leaves. Besides, vertical leaves and those with the mean steep leaf angle of evergreen species could keep their stomata relatively open without a significant burden in terms of water loss by transpiration (Fig. 6). In order to operate near air temperatures, deciduous species should increase transpirational cooling by keeping their

stomatal conductance significantly higher than the evergreen species to compensate for their higher interception of radiation.

Discussion

In the mexical shrubland evergreen species presented an average leaf angle steeper than that of the deciduous species, which suggests that this is an important mechanism by which evergreen species avoid high temperatures and minimize water loss during the dry season. In contrast, deciduous species avoid this condition by shedding their leaves. In a comparison among five western Australian communities, Smith et al. (1998) found that the proportion of species with steep leaf angles and thicker leaves increases as precipitation decreases and light increases among communities. This steep leaf angle pattern has also been reported for Mediterranean species such as *Arctostaphylos* spp. (Shaver 1978), *Quercus ilex* (Burriel et al. 1993), *Heteromeles arbutifolia (*Valladares and Pearcy 1997), and *Silphium terebinthinaceum*, which occurs throughout the prairies of Illinois (Smith and Ullberg 1989). In our study, as an exception, the evergreen species *Gymnosperma glutinosum* (Asteraceae) presented almost horizontal leaf angles. This species is covered by waxes which probably increase reflectance of solar energy as it has been demonstrated in *Dyandra sessilis* by Pearman (1966). Likewise, this species has narrow, needle like leaves which would reduce boundary layer resistances, coupling leaf temperatures more closely to air temperatures.

Functionally, the occurrence of steep leaf angles is related to their effects on water relations, leaf temperature and photosynthesis (Ehleringer and Werk 1986; Rundel 1995; Valladares and Pearcy 1997). The effect of leaf angle on leaf temperature was shown in two of the species studied. The differences of 3 to 5°C in temperature found between vertical and horizontal leaves may have an important effect on transpiration and photosynthesis (Ehleringer and Werk 1986). In this study, horizontally restrained leaves showed lower water potentials after three days than control, vertical

leaves, demonstrating that leaf angle has an important role not only in affecting the interception of irradiance but also in regulating water distribution among foliage units. In agreement with this, Comstock and Mahall (1985) reported that steep leaf angles decrease water stress in *Ceanothus megacarpus* and *C. crassifolius*. The same results have been reported by various authors working in Mediterranean ecosystems (Smith and Ullberg 1989; Valladares and Pearcy 1997). Differences in water potential found here might be seen as minor or moderate, but recent studies are showing that even minor differences in physiological parameters can have profound impacts on plant fitness. For instance, a slight decrease in photochemical efficiency induced by drought, which would have taken as no indication of stress in traditional ecophysiological studies, significantly decreased crucial fitness components in a semiarid plant (Aragon et al. 2008), and slight decreases in stomatal or hydraulic conductances can drastically affect the capacity of woody plants to cope with water limitations (McDowell et al. 2008).

Steep leaf angles are effective in avoiding excessive radiation only if sun elevation angles are also steep. Sun elevation angles are high most of the year in the study area due to its rather low latitude, and even though sun is not at its highest elevation during the dry season it is over 70 degrees above the horizon during this critical period. This sun elevation angle is higher than the average sun elevation angles observed in Mediterranean and other dry areas in temperate zones where photoprotection by steep leaf angles has been well documented (e.g. Ehleringer and Comstock 1987, Valladares & Pugnaire 1999). Changes of 25-30° in leaf angle were sufficient to cause substantial reductions in the total amount of intercepted radiation and led to a 5% reduction in transpiration rates (Comstock and Mahall 1985; Rundel 1995). Since steep leaves were able to maintain low transpiration rates with relatively high stomatal conductances (Fig. 5), internal CO_2 concentration of steep leaves can be high despite drought, allowing for relatively high photosynthetic rates and, thus, leading to a high water use efficiency. Steep photosynthetic surfaces represent, nevertheless, a trade-off between

intercepting enough radiation for photosynthesis and avoiding excessive, potentially harmful irradiance and overheating (Valladares and Pugnaire 1999). In most dry ecosystems, radiation is not limiting for photosynthesis and plants tend to sacrifice opportunities of high rates of carbon gain under optimal conditions for a more conservative water use strategy involving high levels of photoprotection (Ramirez et al. 2006). Steep angles coupled with an evergreen leaf habit have been associated with such a conservative water use strategy in a number of Mediterranean woody species (Mediavilla and Escudero 2003).

In this study we have found extreme water potentials, reaching as low as -8.8 Mpa. This surpasses almost all those reported for chaparral species during the dry season such as *Arctostaphylos glauca* (- 6 Mpa), *A. glandulosa* (- 6.36 Mpa), *Adenostoma fasciculatum* (- 5.6 Mpa), *Ceanothus crassifolius* (- 8.20 Mpa), *Garrya elliptica* (- 6.98 Mpa), *Heteromeles arbutifolia* (- 4.3 Mpa), *Quercus berberidifolia* (- 4.46 Mpa), *Rhus ovata* (- 3.34 Mpa), and *Salvia mellifera* (- 10.24 Mpa) (Miller and Poole 1979; Mooney and Miller 1985; Rundel 1995; Bhaskar et al. 2007). Low water potentials have been related to embolism in different species of the chaparral at different water potentials values ranging from -0.98 to -9.3 MPa (Jacobsen et al. 2005). In the mexical species the low water potentials observed in the unmodified leaves reveals that these species can tolerate severe water-stress conditions.

A tight evolutionary correlation between the minimum seasonal water potential values and the xylem resistance to embolism has been reported in several species of the mexical and chaparral shrublands, indicating the adaptive nature of this correlation (Bhaskar et al. 2007). We suggest that these stressful conditions found in the mexical shrubland since the final part of the Tertiary period (Axelrod 1958; Valiente-Banuet et al. 1998) have constituted a severe environmental factor that is determining the current community assembly. Indeed, our phylogenetic analyses show that the mexical community assemblage is mainly composed of evergreen-plant species that have evolved steep angles in a correlated fashion. From an evolutionary perspective these lineages that originated in forests

during the Tertiary probably could survive the shift from the mesic Tertiary to the unusually dry Quaternary by producing smaller, thick leaves with a more inclined leaf orientation as a common response to dryness. Considering that in many woody plants plasticity in the inclination and orientation of the units of the foliage has been associated with the capture of diffuse rather than direct radiation, leaf angle has been considered as a variable trait, readily subject to selection to improve plant carbon balance (Ackerly and Bazzaz 1995; Valladares and Pearcy 1998). Enhanced penetration of diffuse radiation within the crown of the plant increases whole plant carbon gain by distributing global radiation among the leaves more efficiently from a photosynthetic point of view. Consequently, under the new stressful conditions experienced during the Quaternary and with no light limitations, the evergreen species studied oriented their leaves to reduce heat loads at midday, decreasing the risk of over-heating and photoinhibition (Valladares and Pugnaire 1999), and at the same time maximizing the distribution of light among leaves and the potential carbon gain associated to it. However, all these evergreen species remained broadleafed, which contrasts with those species from more stressful habitats than the mexical whose leaves are also steep but they became almost cylindrical and smaller (Smith et al. 1997; Smith & Hughes, 2009). The over-representation of a particular trait in an ecological community may be the outcome of ecological sorting processes and/or trait evolution driven by the environmental factor (Webb et al. 2002). The climatic change represented an unprecedented change towards aridity and the new climate could have filtered pre-existing physiological strategies, like those of evergreen plants (Valiente-Banuet et al. 2006). The maintenance of ancestral traits in ancient lineages is common in the mexical and in other arid environments such as the Mediterranean type ecosystems (Herrera 1992; Verdú et al. 2003; Ackerly 2004). Alternatively, plants may have evolved such strategies within current communities as a response to the new climate. A comparison of our results with those reported in sclerophyllous vegetation in Mediterranean ecosystems suggests that water stress during six to seven months per year is a common selective force for woody plants dwelling

in these two ecosystems. Since examples of both stasis and evolutionary divergence in physiological traits have been documented (Bhaskar et al. 2007), our study reveals that both ecological sorting and trait evolution may have contributed to the functional diversity of the mexical plant community.

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Figure legends

Fig. 1. Ombrothermic diagram of the nearest climatic station to the study site: Chapulco, Puebla. (data from García, 1988).

Fig. 2. Frequency distribution of leaf angles of the adaxial side of the leaf with respect to the horizontal in evergreen and deciduous species in the Tehuacan Mexical. Largest bar in the circles represents the mean ± S.D. values.

Fig. 3. Phylogenetic tree of the mexical study species. Branch lengths are proportional to Myr following the scale shown down-left. Leaf habit (E=Evergreen; D=Deciduous) and leaf angle (mean ± SD) for each species is shown.

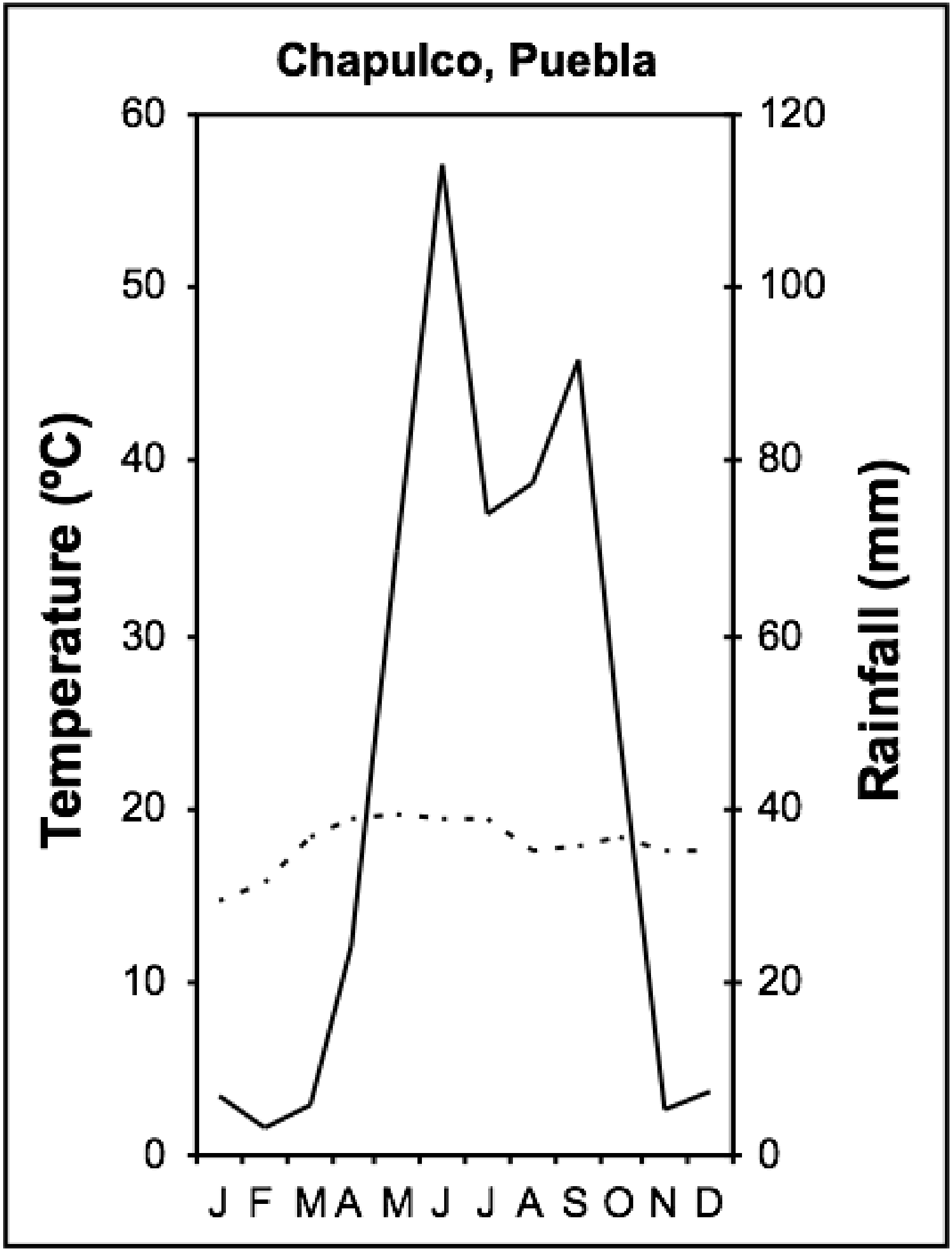
Figure 4. Comparison of mean midday water-potentials (MPa) of five evergreen-sclerophyll species for vertical (control) and horizontally restrained leaves (horizontal) during the dry season in the Tehuacan Mexical.

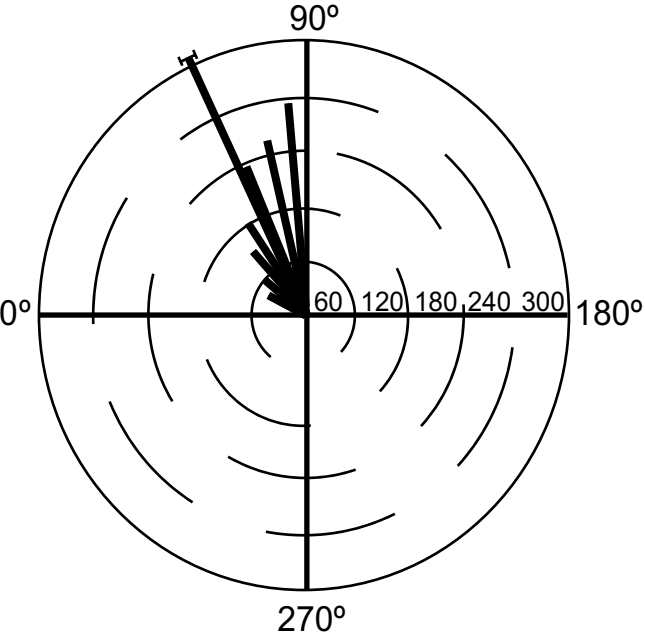
Fig. 5. Daily course of leaf temperature in (A) *Quercus sebifera* and in (B) *Rhus standleyi* during the dry season in the Tehuacan Mexical.

▲ horizontal leaves, ●vertical leaves, ■ Air temperature.

Fig. 6. Leaf temperature (left panel) and transpiration (right panel) as functions of leaf angle and stomatal conductance for evergreen woody plants at midday during the dry season in the Tehuacan mexical. Calculations are made with real leaf elevation angles (E), horizontal (H), and vertical leaf

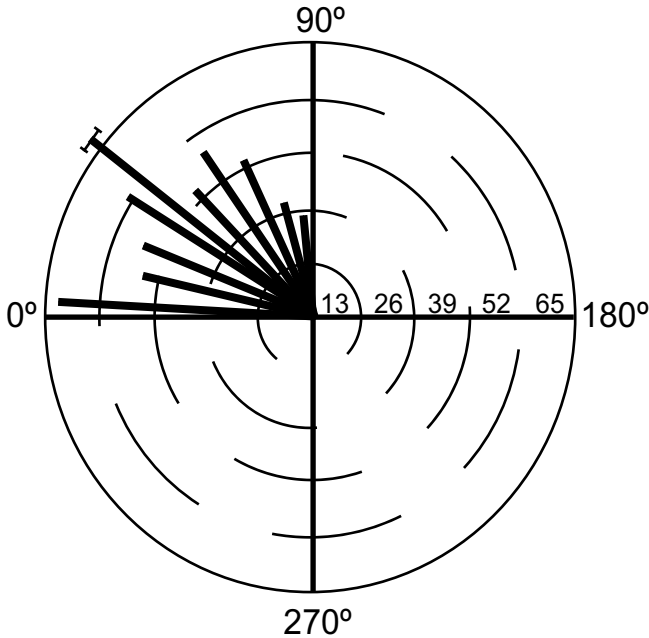
elevation angles (V). Woody deciduous plants (D) do not have leaves during the dry season but they are placed in the graph to facilitate comparisons and their estimated range of leaf conductances is also shown (dashed error bars). Two conditions, mild and windy (A) and hot and still (B, see Methods), were simulated based on field measurements, and dotted lines on left panel indicate air temperatures for each simulated conditions. Bars represent standard errors.


Chapulco, Puebla
Temperature (°C)
Rainfall (mm)
60
50
40
30
20
10
0
120
100
80
60
40
20
0
J F M A M J J A S O N D



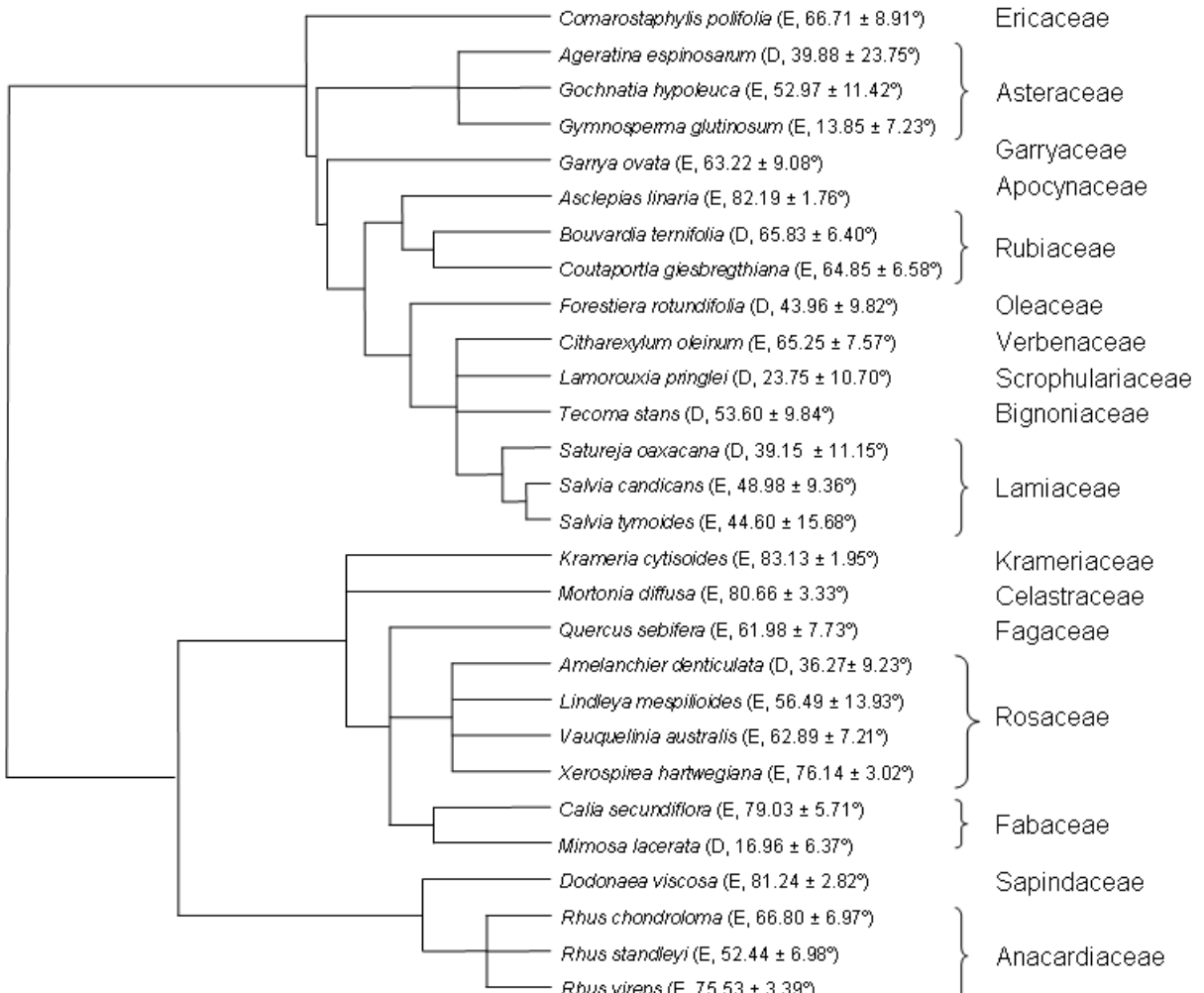
Mean 62.87 ± 22.17

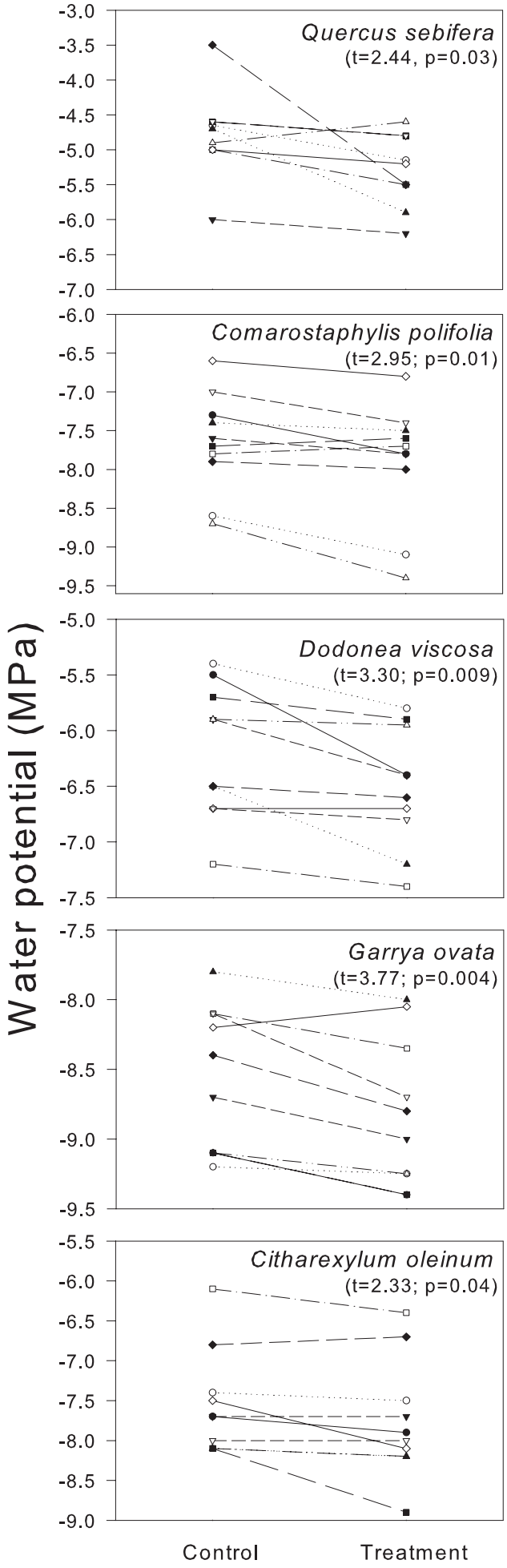
Evergreen species

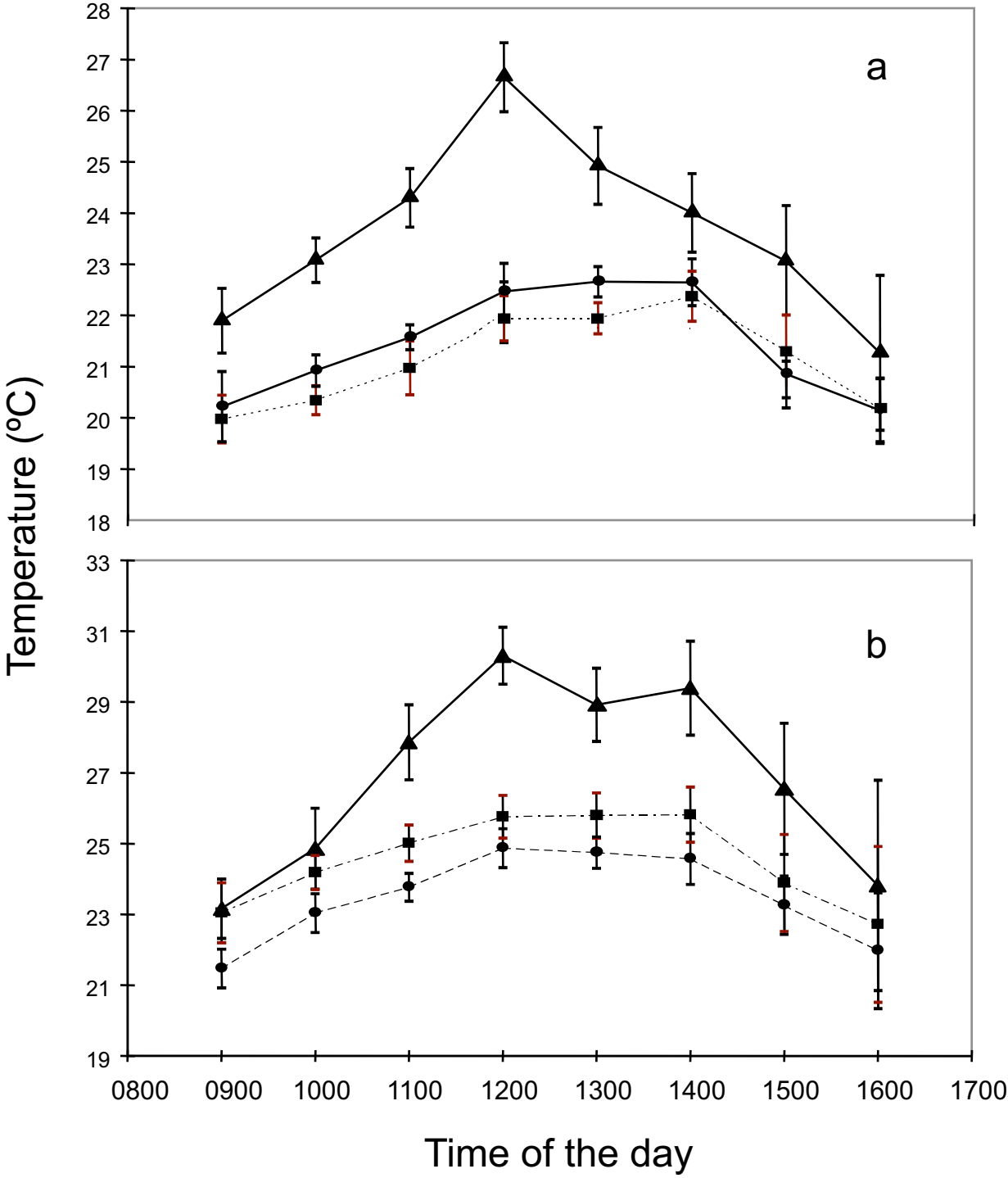


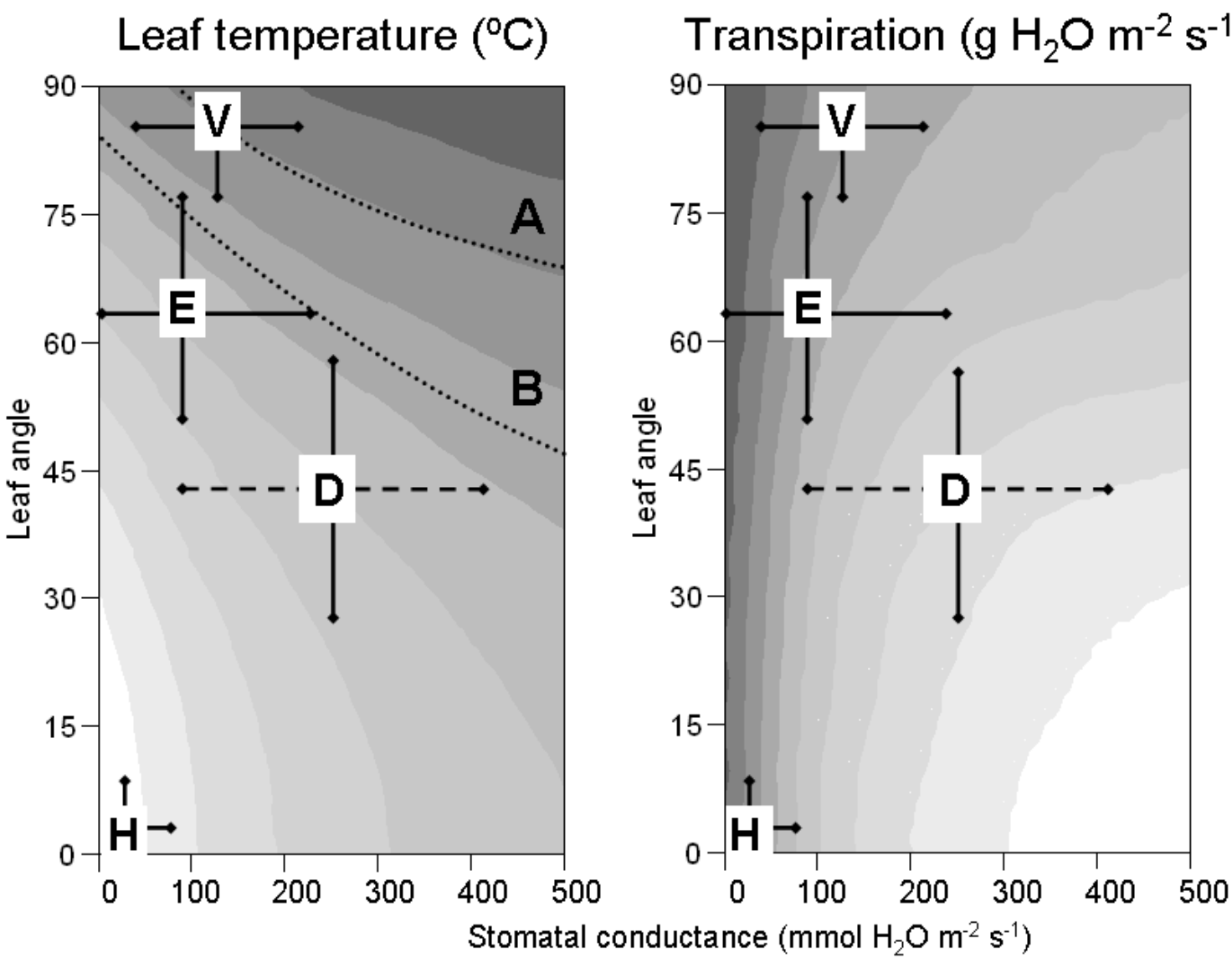
Mean 39.98 ± 26.07

Deciduous species


Comarostaphylis polifolia (E, 66.71 ± 8.91°)
Ericaceae
Ageratina espinosarum (D, 39.88 ± 23.75°)
Gochnatia hypoleuca (E, 52.97 ± 11.42°)
Gymnosperma glutinosum (E, 13.85 ± 7.23°)
Asteraceae
Garrya ovata (E, 63.22 ± 9.08°)
Garryaceae
Asclepias linaria (E, 82.19 ± 1.76°)
Apocynaceae
Bouvardia ternifolia (D, 65.83 ± 6.40°)
Coutaportla giesbregthiana (E, 64.85 ± 6.58°)
Rubiaceae
Forestiera rotundifolia (D, 43.96 ± 9.82°)
Oleaceae
Citharexylum oleinum (E, 65.25 ± 7.57°)
Verbenaceae
Lamorouxia pringlei (D, 23.75 ± 10.70°)
Scrophulariaceae
Tecoma stans (D, 53.60 ± 9.84°)
Bignoniaceae
Satureja oaxacana (D, 39.15 ± 11.15°)
Salvia candicans (E, 48.98 ± 9.36°)
Salvia tymoides (E, 44.60 ± 15.68°)
Lamiaceae
Krameria cytisoides (E, 83.13 ± 1.95°)
Krameriaceae
Mortonia diffusa (E, 80.66 ± 3.33°)
Celastraceae
Quercus sebifera (E, 61.98 ± 7.73°)
Fagaceae
Amelanchier denticulata (D, 36.27± 9.23°)
Lindleya mespilioides (E, 56.49 ± 13.93°)
Vauquelinia australis (E, 62.89 ± 7.21°)
Xerospirea hartwegiana (E, 76.14 ± 3.02°)
Rosaceae
Calia secundiflora (E, 79.03 ± 5.71°)
Mimosa lacerata (D, 16.96 ± 6.37°)
Fabaceae
Dodonaea viscosa (E, 81.24 ± 2.82°)
Sapindaceae
Rhus chondroloma (E, 66.80 ± 6.97°)
Rhus standleyi (E, 52.44 ± 6.98°)
Rhus virens (E, 75.53 ± 3.39°)
Anacardiaceae
10


Water potential (MPa)
Quercus sebifera
(t=2.44, p=0.03)
Comarostaphylis polifolia
(t=2.95; p=0.01)
Dodonea viscosa
(t=3.30; p=0.009)
Garrya ovata
(t=3.77; p=0.004)
Citharexylum oleinum
(t=2.33; p=0.04)
Control
Treatment


a
b
Temperature (ºC)
Time of the day
28
27
26
25
24
23
22
21
20
19
18
33
31
29
27
25
23
21
19
0800
0900
1000
1100
1200
1300
1400
1500
1600
1700



ºC	A	B
	34	48
	33	46
	31	44
	30	42
	29	40
	28	38
	27	36
	26	34
	25	32
	24	30

g H_2O m^{-2} s^{-1}	A	B
	0.14	0.18
	0.12	0.16
	0.10	0.14
	0.08	0.12
	0.06	0.10
	0.04	0.08
	0.03	0.06
	0.02	0.04
	0.01	0.02
	0	0